MECHANICS OF THE LIGAMENT IN THE BIVALVE SPISULA SOLIDISSIMA IN RELATION TO MODE OF LIFE

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The bivalve shell is closed by the action of adductor muscles. These, the largest muscles in any bivalve, have no single antagonists but can be stretched by several mechanisms, which include the elasticity of the horny hinge ligament and several kinds of hydraulic systems. The relative importance of each method varies in different types of bivalves.

The elastic ligament connects the shell valves dorsally and is under strain when the valves are closed. The strain is tensile in the outer part of external hinge ligaments, but corresponds to compression in internal ligaments, or resilia, and in the inner layer of others. Functional morphology and development of the ligament have recently received considerable study (Owen, Trueman and Yonge, 1953; Owen, 1953, 1958, 1959a, 1959b; Trueman, 1949, 1950, 1951, 1953, 1954; Yonge, 1953, 1955, 1957), and the detailed investigations of Trueman have included mechanical analyses of the operation of the ligament in certain genera, notably *Ostrea, Pecten* and *Mya* (Trueman, 1951, 1953, 1954). The force derived when the ligament is under strain tends to open the valves, *i.e.,* acts against the adductor muscles, and Trueman (1953, 1954) terms this the "opening moment" of the ligament.

The forces which can be grouped as "hydraulic" means of shell opening are of two kinds, derived respectively from compression of (a) body-fluids in the "haemocoele," and (b) water in the mantle-cavity. The first category includes the protrusion of the foot, used to force the shell valves apart in adult *Cardium edule* and *Anodonta cygnea,* and in the young of many bivalves including *Spisula solidissima,* but could also include the distension of fused ventral edges of the mantle. The second, water pressure, is used particularly in those bivalves where extensive fusion of the mantle margins has occurred (Yonge, 1955, 1957). Hunter (1949) showed that the method of boring in *Hiatella gallicana* depended on the shell valves being forced apart by water pressure inside the mantle cavity. The use of water pressure in the mantle cavity, for extending the siphons by contraction of the adductor muscles, was later investigated in detail in *Mya arenaria* (Chapman and Newell, 1956; see also Chapman, 1958).

Among the larger burrowing bivalves, *Mya arenaria* and *Spisula solidissima* offer a number of contrasts in their modes of life. The former is a sedentary "deep-burrower," almost immobile in adult life, the latter an active burrower, one of the so-called "surf-clams" living just within the substrate. The mechanics of the

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ligament (Trueman, 1954) and the hydraulics of the mantle cavity (Chapman and Newell, 1956) have been investigated in *Mya*. In spite of other differences, *Spisula* has a ligament structurally similar to that of *Mya*. The data presented in the present paper result from an investigation of the mechanical characteristics of the ligament in *Spisula solidissima* at Woods Hole, and include hysteresis curves and determinations of the opening moment in a range of growth stages (sizes). These data are then discussed in relation to the earlier work of Trueman and others, with special reference to the marked differences between *Spisula* and *Mya*.

MATERIAL AND METHODS

Specimens of the surf-clam, *Spisula solidissima*, were obtained from a locality on the shores of Martha's Vineyard known to Mr. Milton B. Gray and one of the present authors (D.C.G.). All the material used was collected by hand from
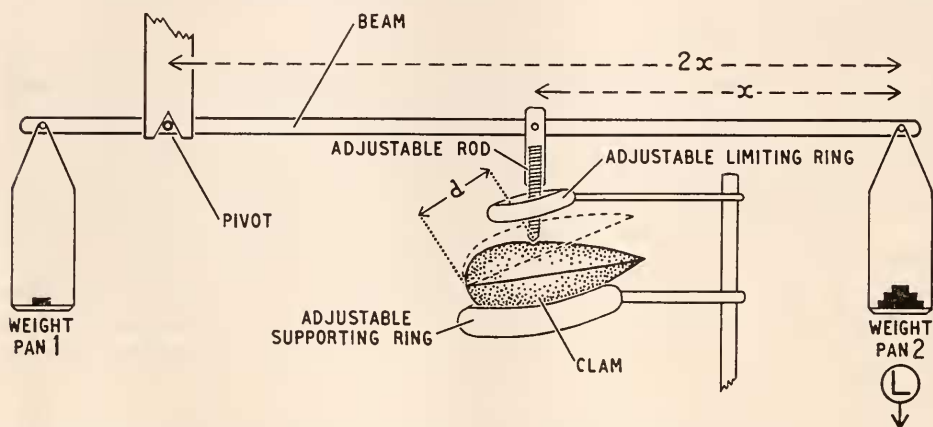

FIGURE 1. The apparatus used to measure the mechanical characteristics of the ligament in *Spisula* (slightly modified from Trueman, 1951, 1953). The pivoted beam is counterbalanced by weights in pan 1, and is so arranged that the force applied through the adjustable rod to the centroid of the upper valve is twice the load (L) in pan 2. The actual moment applied to the ligament also depends on the distance (d) between the pivotal axis of the ligament and the point of application (*i.e.,* the valve centroid). The diagram is not to scale. For further details, see text.

depths of 10–13 feet (3–4 m.) by D.C.G., using a face mask and snorkel, and a range of sizes was deliberately selected to include specimens of the largest clams in the population. In this locality, clams occur up to 18 cm. maximum shell length, with a wet weight of 860 g. (with shell, but drained of mantle cavity water). Little or nothing is known of the age of such clams. The bottom deposits are of relatively clean, coarse-grained sand (see below), and the clams are living within the first 12 cm. of the substrate (*i.e.,* with only the posterior edges of the shell and the short tentacle-fringed siphons showing). A typical water temperature by day in summer at the bottom would be 19.5° C. (surface water, 20° C.), and the experimental work on the ligament was done at room temperatures from 22.0 to 24.5° C.

Hysteresis curves and closing and opening moments for each ligament were

determined on clams in which all the muscular and other tissues connected to the right shell valves had been cut. This was done with the clam so held that the valves could not gape beyond an angle natural in life. With the left valve firmly supported, loads were applied to the centroid of the right valve by means of a hinged counterbalanced beam (see Figure 1.) This apparatus is essentially similar to that used by Trueman (1951, 1953) for measurements on the ligaments of *Ostrea, Pecten* and other bivalves and is so arranged that the actual load applied to the centroid of the upper (right) valve is twice the load (L) in pan 2. Thus each moment applied to the ligament, M in g. mm., can be derived from the expression $M = d\ (2L + W)$, where d is the distance (in mm.) from the point of application (the valve centroid) to the pivotal axis of the ligament between the shell valves, L is the applied load and W the weight of the upper (right) valve (both in grams). Angles of gape, both in living clams, and during the loading experiments, were determined by measurement of the maximum distance between the ventral edges of the valves with an internal caliper. This distance was used with the shell height, measured from the hinge line to the ventral edge, to derive an angle in radians, later converted to degrees (see Table I). The closed volume of each clam was subsequently determined by displacement weighings, the cleaned valves being filled with plaster of paris.

Results

In most experiments, before loading of the ligament was begun, the valves had been held for some time at an angle of gape about equal to the gape in life of that particular clam. The load applied to the right valve was then increased gradually until the valves were firmly closed, angle of gape and corresponding load being noted at appropriate intervals. The applied load was then gradually decreased until the valves re-opened, and this unloading continued until the natural gape was again approached. Final detection of the points of closing and of opening of the valves was by use of a feeler gauge of thin card at several points around the ventral margin. This loading and unloading sequence was repeated. (In most cases two to three runs per clam sufficed—as the results were extremely consistent, particularly as regards the load at the point of re-opening.) It was found experimentally that the load at opening had not changed several hours after excision of the living tissues. In practice the loading and unloading experiments on each clam were completed within 15–20 minutes. The loads (L) corresponding to each measured gape were then expressed as moments (M) applied to the ligament, using $M = d(2L + W)$. Each gape was converted to an angle in degrees. When the applied moments are plotted against the angles of the loading and unloading sequence for each clam, hysteresis curves result. Figure 2 shows such plots of angle of gape against moment applied for two of the 35 clams of the main experimental series, one (no. 3) very large and one (no. 10) relatively small. Since the ligament is under maximum stress when the valves are completely closed, this "zero gape" corresponds to the maximum force applied. It is therefore convenient to show the closed position (with maximum applied moment) at the right of each graph (as was done by Trueman, 1953, for similar results). Certain features are common to all such curves. Increasing load decreases the angle of gape (section a) until the valves are closed (zero gape—at the right of each figure). The load

which just closes the valves must be somewhat decreased before the valves re-open (vertical part between **a** and **b** at the right of the figure). Decrease of load then gives increasing gape (the first unloading curve—**b**), until the "natural gape" is again approached, when the load is increased again (second loading curve—**c**) to

TABLE I

Natural and maximum angles of shell gape, mean loads at opening, and calculated opening moments for the ligament, in Spisula

Animal No.	Volume, V, ml.	Gape in life, degrees	Maximum gape with *no* load, degrees	Mean load at opening, L, g.	Right valve weight, W, g.	$(2L+W)$, g.	Centroid of shell to centroid of ligament, d, mm.	Opening moment, $M=d(2L+W)$, g. mm.	M/V, g. mm. per ml.
1	218	8.3	18.2	1260	64	2584	46	118,864	545
2	380	8.2	25.0	2240	118	4598	54	248,292	653
3	761	10.5	23.2	2930	191	6051	66	399,366	525
4	105	10.2	25.2	598	27	1223	43	52,589	501
5	290	7.0	24.1	1953	88	3994	48	191,712	661
6	449	9.0	22.1	2963	151	6077	53.5	325,120	724
7	553	8.3	22.3	2188	182	4558	64	291,712	528
8	634	8.4	18.1	3277	213	6767	58	392,486	619
9	160	9.6	22.9	1129	44	2302	37	85,174	532
10	118	8.1	19.3	773	31	1576	37	58,312	494
11	465	8.8	18.1	2630	161	5421	60	325,260	699
12	452	8.1	20.1	2735	135	5605	60	336,300	744
13	336	9.6	24.1	2095	115	4305	51.5	221,708	660
14	445	9.7	19.4	2457	126	5040	55	277,200	623
15	479	9.0	21.9	2195	141	4531	60	271,860	568
16	392	9.2	22.2	2288	116	4692	55	258,060	658
17	549	9.1	20.3	2340	169	4849	62	300,638	548
18	459	9.1	20.0	2887	145	5919	58	343,302	748
19	389	11.0	25.8	2265	123	4653	52	241,956	622
20	404	8.2	20.4	2275	136	4686	59	276,474	684
21	219	7.4	22.3	1255	65	2575	51.5	132,613	606
22	143	7.5	24.3	803	40	1646	41	67,486	472
23	179	9.8	20.7	1207	59	2473	40.7	100,651	562
24	244	8.2	23.0	1703	71	3531	47	165,957	680
25	344	8.3	23.1	1835	103	3773	56	211,288	614
26	296	8.3	25.2	1405	89	2899	50	144,950	490
27	385	9.7	28.7	2563	112	5238	54	282,852	735
28	426	8.6	23.2	2183	124	4490	55	246,950	580
29	200	6.7	22.5	945	50	1940	44	85,360	427
30	237	8.0	20.7	1505	58	3068	48	147,264	621
31	219	8.8	20.4	1355	57	2767	47	130,049	594
32	214	7.7	23.1	1383	60	2826	46	129,996	607
33	358	9.6	21.5	1900	110	3910	53	207,230	579
34	423	7.3	23.6	2335	142	4812	58	279,096	660
35	295	7.2	18.4	2150	100	4400	50	220,000	746

Mean of M/V = 608.83 g. mm. per ml.

shell closure, then again decreased (second unloading curve—**d**). Subsequently the maximum angle of gape (with *no* load) was determined for each clam, and this value is shown connected to each second unloading curve (**d**) in Figure 2. In successive loadings the applied moment for any given angle of gape is reduced,

i.e., the second loading curve (**c**) lies to the right of the first (**a**). On the other hand, successive unloading curves (**b** and **d**) are closely similar, and the applied moment when the valves first re-open is nearly constant.   Trueman (1953) has pointed out that the size of the area enclosed by such hysteresis loops (*i.e.,* between loading and unloading curves) provides a measure of the efficiency of a ligament as regards its elastic properties.   The smaller the area, the less "damping" occurs: the more efficient is the ligament.   Hysteresis loops for ligaments of *Spisula solidis-*
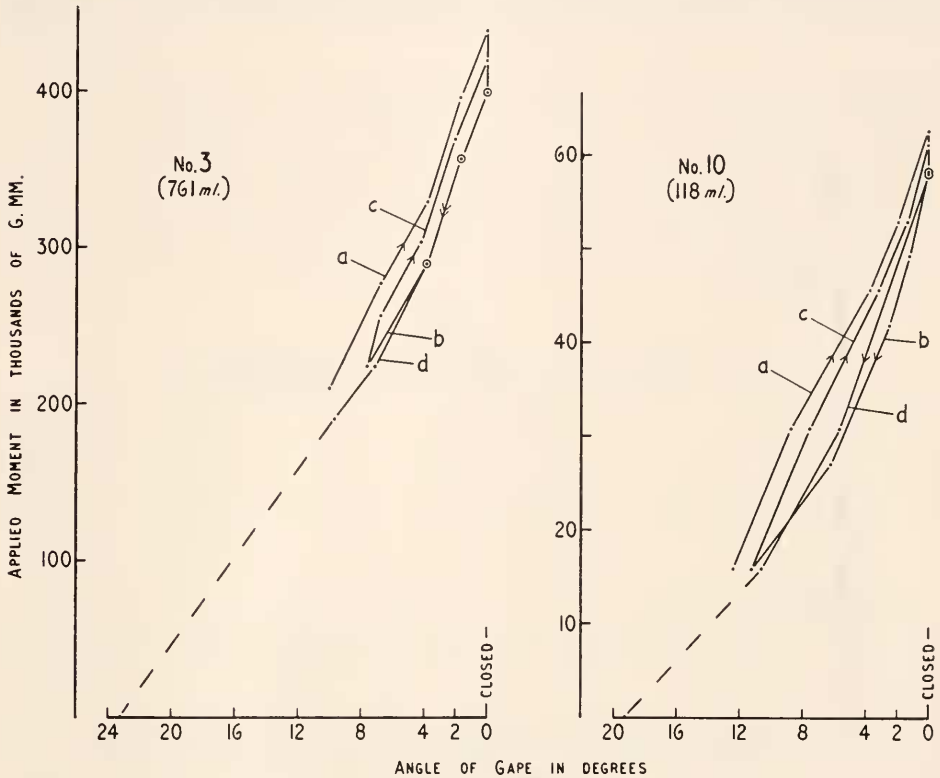

FIGURE 2.   Graphs showing the relation between moments applied to the ligament of *Spisula* and the resultant angles of gape of the valves.   The shell valves are completely closed at the right of each graph (at maximum applied moment).   Each clam was subjected to increasing load (**a**), followed by unloading (**b**), a second loading (**c**) and a second unloading (**d**).

sima can be compared in this respect with those published by Trueman (1953). The ligament of *Spisula* would appear to be more efficient than those of *Mya arenaria* and *Anodonta cygnea,* but considerably less efficient than those of *Pecten* and *Chlamys.*

Hysteresis curves are not provided here for all 35 clams of the main series but their mean loads at opening (always consistent values) and their calculated opening moments are shown in Table I.   It should be noted that, in these experiments on *Spisula,* each actual load at opening was measured, whereas many of the figures

for the opening moments of different bivalves presented by Trueman (1953, 1954) are estimated from closing loads, which alone were measured.   In the present work on *Spisula,* at least, it is clear that the load at opening gives a much more consistent value for each ligament than the closing load.   Considerable manipulation of any ligament, provided the valves were kept within a "natural" angle of gape, did not appreciably alter the opening load.   Even repeated "clapping" of the valves at intervals of about a second produced little change in this measure of elasticity of the ligament.   Similar constancy was remarked by Trueman (1953) in experiments on *Chlamys, Pecten,* and *Anodonta.*
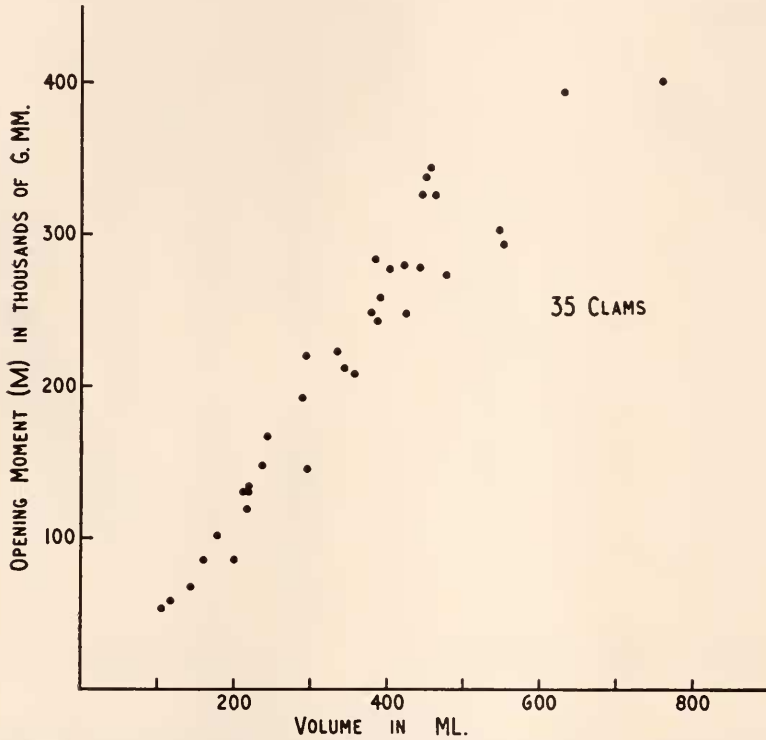

FIGURE 3.   Plot, for *Spisula* of different sizes, of the opening moments exerted by the ligament in relation to the volume of each whole clam.   For further explanation, see text.

In Table I the weight of the right shell valve (W) and the distance from the axis of the ligament to the point of application of the load (d) are both shown. From these and the mean load at opening (L), the opening moment (M) is derived using $M = d(2L + W)$.   The opening moment of the ligament varies with the size of the clam (see Table I).   In some cases, Trueman has related closing and opening moments to the surface area of the valves (Trueman, 1951, 1954), and in others to total shell volume (Trueman, 1953).   For the main series of *Spisula* opening moments are plotted against whole volumes in Figure 3.   The relationship is satisfactory, and so in the last column of Table I the results are expressed as opening moments per unit volume (*i.e.,* M/V in g. mm. per ml.).   The mean value

for all the determinations on *Spisula* is 608.83 g. mm. per ml. (range = 427–748, s.d. = 83.02 g. mm. per ml.). This is comparable to values for the most powerful ligaments already measured: those of *Mytilus edulis* and *Cyprina islandica* (660 and 550 g. mm. per ml., Trueman, 1953); and is considerably greater than that for *Mya arenaria* (174, Trueman, 1954) and those for the efficient swimmers, *Pecten maximus* and *Chlamys opercularis* (160 and 142, Trueman, 1953). Thus, in the range of bivalves already studied, the strength of the ligament in *Spisula solidissima* is comparatively great, and its "efficiency" is at an intermediate level. More detailed comparisons between *Spisula* and *Mya arenaria* are made in the discussion below.

Table I also shows, for each clam, the angle of gape of the shell valves measured in life, and the maximum angle of gape (under no load) measured after completion of loading and unloading cycles. For *Spisula* the mean gape in life is 8.6 degrees, and the mean maximum gape 22.1 degrees. This value for the maximum gape is less than that for *Pecten* (approx. 32 degrees) and greater than for *Mytilus* and *Ostrea* (both approximately 10 degrees). As shown for the larger clam in Figure 2, this maximum gape usually corresponds fairly well to an extrapolation of the

TABLE II

*Particle size in substrates occupied by Spisula solidissima and Mya arenaria:
percentage of sample by weight in each size category*

Size range of particles in mm.	<.062	.062–.125	.125–.25	.25–.5	.5–1	1–2	>2
Mya soil	.003	.11	11.68	60.96	9.19	5.97	12.07
Spisula soil	.008	.003	.38	17.34	81.6	.59	—

loading curves, *i.e.*, the applied moment (or, in life, the force exerted by contraction of the adductor muscles) remains more or less constant per degree of gape. In comparing *Spisula* with *Mya* in terms of the mechanical properties of their ligaments, and their very different modes of life, it will be necessary to refer to the types of substrate in which they live. *Spisula solidissima* usually occurs in clean, coarse-grained sand—a surf-shore "shifting-sand." The muddy soil inhabited by *Mya* is usually more consolidated. Mechanical analysis was carried out on samples of sand from the *Spisula* locality, and of soil from a *Mya* bed in the Woods Hole area, and the results appear in Table II. The *Mya* substrate contained some gravel and small stones which accounts for there being 12% of the sample in the > 2 mm. fraction. Apart from this, most of the *Mya* soil lies in the 0.25–0.5 mm. range, while the bulk of the *Spisula* substrate is in the 0.5–1 mm. range. From these samples, *Spisula* seems to live in a significantly coarser and much more uniform substrate. No measurement of the mechanical resistance of these soils was made in the field, but fingers can be moved very readily through the *Spisula* sand, but only with some difficulty in a *Mya* soil.

DISCUSSION

As Trueman has pointed out, if the opening moment of the ligament is measured in a range of bivalves, and then assessed in terms of individual size, the range of

values cannot be directly related to habitat substrate alone. In a few bivalves, notably attached forms (*e.g., Ostrea,* Trueman, 1951) and actively-swimming forms (*e.g., Pecten,* Trueman, 1953), the ligament is clearly the principal mechanism used to open the valves. As noted above, various "hydraulic" means of shell-opening are relatively more important in other bivalves. In *Mya arenaria,* a deep-burrowing bivalve, Trueman (1954) found that the opening moment of the ligament is inadequate to open the valves when the animal is buried in a typical substrate. Chapman and Newell (1956) showed that the extension of the siphons in *Mya arenaria* depends on water pressures generated by contraction of the adductor muscles acting on the enclosed water of the mantle cavity. Conversely, retraction of the siphons, with all mantle openings closed, will result in opening of the shell valves.

Turning to consideration of *Spisula solidissima,* the present work shows that its ligament is much stronger than that of comparable *Mya arenaria.* The mean opening moment for *Spisula solidissima* is 609 g. mm. per ml., while that for *Mya* is 174 g. mm. per ml. (Trueman, 1954). The extent of "damping" in a complete loading and unloading cycle is also less in the ligament of *Spisula,* the elasticity of which is thus more "efficient" in this respect. In contrast, it is unlikely that hydraulic forces are as important in shell-opening in *Spisula* as in *Mya.* In *Spisula solidissima* the ventral edges of the mantle margins are structurally free (*i.e.,* unfused) between the pedal opening and the base of the siphons. As noted by Yonge (1948) and Kellogg (1915) functional (as distinct from structural) enclosure of the mantle cavity in *Spisula* is produced by close apposition of the free mantle edges posterior to the pedal opening. Although this functional ventral closure is undoubtedly effective in relation to the feeding and cleansing mechanisms of the clams, it is unlikely to be as efficient as the muscular fused ventral surface of the mantle of *Mya* in allowing use of a "hydraulic skeleton." Further, in those bivalves in which increase of water pressure in the mantle cavity can be used to open the valves, the additional capacity for water provided by proportionately large muscular siphons is often clearly important. In an investigation of the boring mechanism in *Hiatella,* Hunter (1949) noted that the increased pressure in the mantle cavity, and the consequent forcing apart of the shell valves, was brought about by the closure of all the openings of the mantle, followed by a retraction of the siphons. Thus, in *Spisula solidissima,* with the mantle lobes effectively unfused along their ventral margins, and with relatively small, inextensile siphons, hydraulic forces utilizing the water of the mantle cavity are unlikely to be important in shell-opening. As noted above, another type of hydraulic mechanism which can be involved in opening movements of the valves depends on body fluids within the foot and pallial edges. The importance of changes in the distension of these organs has not been investigated quantitatively in *Spisula solidissima,* but observations suggest that pedal extrusion is relatively less important as a component of the shell-opening forces in specimens in the present size-range (shell-lengths 9.5–18.0 cm.) than in young animals (< ca. 3.0 cm. long) of the same species.

The resistance of typical substrate to the opening of the clams' valves must also be considered. Trueman has already experimented with *Mya* valves in "soils" of different physical characteristics and provides (1954) some measurements of resistance. As noted above, the *Spisula solidissima* were obtained from a clean,

coarse-grained sand, very different from the kind of muddy soil inhabited by *Mya* in the Woods Hole area.   Trueman's range of soils did not include any with the surf-shore "shifting-sand" characteristics of the present *Spisula* locality.   In a qualitative assessment of the case, although the grain size is larger, the *Spisula* substrate is markedly less resistant to any movement than a *Mya* soil.   Trueman (1954) also demonstrated that, in any soil, a greater depth of burial caused an increased resistance to shell-opening.   Thus the more powerful ligament of *Spisula* works against less resistance than the ligament and hydraulic forces of *Mya*.   It is reasonable to deduce, therefore, that in *Spisula solidissima*, the ligament provides the most important of the forces acting against the adductor muscles and opening the valves.   Thus, in the sedentary, deep-burrowing *Mya*, hydraulic means are important in shell-opening and the ligament is relatively weak, while in the active surface-burrowing *Spisula*, the ligament is relatively powerful and hydraulic forces less important.

In *Hiatella*, with a closed mantle cavity, Hunter (1949) noted that the two adductor muscles could act as antagonists to each other, *i.e.*, independently either the anterior or the posterior end of the shell could be closed.   In mediating this movement of the valves about a dorso-ventral axis, the water enclosed in the mantle cavity is obviously important.   Such movements also do occur in *Mya arenaria*, though they were not reported by Chapman and Newell (1956).   In the course of the present work it was noted that similar rocking movements (implying alternate contraction of anterior and posterior adductor muscles) could occur to a slight extent in *Spisula solidissima*, even with the siphons open.   In this case the ligament itself must mediate the apparent muscle antagonism.

A final matter concerns the inter-relationships of certain burrowing bivalves. In his published survey of various bivalves, Trueman (1953) gives the opening moment of the ligament for only one species of the family Mactridae, *Lutraria lutraria*.   This species is a highly modified deep-burrower, with massive fused siphons.   Trueman obtained a value for *L. lutraria*, admittedly from 8 specimens only, of 265 g. mm. per ml.   This value is high compared to that for *Mya* (174 g. mm. per ml., Trueman, 1954) though not as high as the present mean value for *S. solidissima* (608.8 g. mm. per ml.).   The explanation may be phyletic.   It is usually agreed that those bivalves more highly modified for deep-burrowing (*e.g., Mya, Panope* and *Lutraria*) and for boring (*e.g., Hiatella, Pholas, Petricola*) are derived from less specialized shallow-burrowing forms.   As Yonge (1948, 1951, 1957 and other papers) has elucidated, the structural and functional adaptations associated with deep-burrowing in bivalves are clearly polyphyletic, and their similarities reflect convergence.   Yonge (1948) notes that as a result of its descent from the shallow-burrowing Mactridae, possibly from a form resembling certain *Spisula* spp., the mantle-cleansing mechanisms of *Lutraria* are very unlike those of *Mya*, despite the similarity of external form and habit in the two genera.   It can now be postulated that the mechanical properties of the ligament in *Lutraria lutraria* are unlike those of *Mya arenaria*, again as a result of phyletic derivation—in this case from a form with a relatively powerful ligament, like that presently possessed by *Spisula solidissima*.

Gray of Woods Hole for help in obtaining the material, and Myra Russell Hunter for checking many of our calculations.

SUMMARY

1. The mechanical characteristics of the ligament in *Spisula solidissima* have been investigated and, for a range of sizes, hysteresis curves prepared and opening moments calculated.

2. In this species, the opening moment of the ligament can be related satisfactorily to the volume of the clam, and a mean value per unit volume of 608.8 g. mm. per ml. was determined.

3. The mean angle of gape in life of the shell valves of *S. solidissima* is 8.6 degrees, and the mean maximum gape (under no load) is 22.1 degrees.

4. Compared with the structurally similar ligament of *Mya arenaria,* that of *S. solidissima* is about 3.5 times more powerful (in terms of opening moments), and also more "efficient" (as measured by the "damping" of its elasticity in hysteresis loops). Clearly the ligament in *Spisula* provides the most important antagonist to the contraction of the adductor muscles, while in *Mya* water pressures generated in the mantle cavity are important.

5. These mechanical differences reflect the modes of life of the two clams: *Spisula* is one of the so-called "surf-clams," actively maintaining itself just within an unstable substrate; *Mya* is a sedentary "deep-burrower," almost immobile in adult life.

6. A phyletic explanation is suggested for conditions in the deep-burrowing mactrid *Lutraria lutraria,* where the ligament is about 1.5 times more powerful than that of *Mya,* despite their similarities in external form and habit. *Lutraria* is probably derived from a mactrid resembling *Spisula solidissima* and having a powerful ligament.

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